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Modelling the beginning and end of a planktonic life stage – the distribution of cod eggs and settled juveniles in the North Sea

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As a stock close to the southern limit of the species' range, the North Sea cod stock may be among those most affected by future climate change. Direct, as well as indirect effects of climate forcing may have the greatest effects on early life stages. We here present our examination of the distribution of cod (*Gadus morhua*) at the beginning and at the end of the planktonic life stage. The distribution of cod eggs was modelled with Generalized Additive Models (GAMs) on the presence/absence, as well as the non-zero abundance. For comparison, the egg distribution of haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*) and plaice (*Pleuronectes platessa*) were examined likewise. Findings indicated that in the egg stage, the environment is more important for the probability of occurrence, while abundance is more under the control of spatial dependency. Modelling the potential habitat of newly settled 0-group cod, based on presence/absence alone, identified temperature, salinity, bottom depth and geographic position as the core descriptors of the settlement distribution. The habitat models had fairly good predictive power on the sub-decadal scale, but were found lacking on a longer time scale. Effects of climate change may be complex, giving some species and life stages within the same species an advantage, while others suffer detrimental effects.

Keywords: Fish eggs, Juvenile Fish, Settlement, Cod, Habitat model, Geographic distribution

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Introduction

During the 20th century the North Sea cod (*Gadus morhua*) stock underwent two major events. Firstly the 'gadoid outburst' from 1969 (Hislop, 1996) to the mid-1980s. Secondly, a steep decline in SSB following the outburst and sometimes termed a regime shift (Beaugrand, 2004), hitting a record low in SSB in 2006 (ca. 30,000 t; ICES, 2010). Likewise, recruitment was low since the mid-1980s (Beaugrand *et al.*, 2003). While the consequence of both events is clear, causes are still debated. Some studies suggested variations in available prey during the larval and juvenile phase (Beaugrand *et al.*, 2003; Cushing, 1984), while others suggested direct and indirect effects of Sea Surface Temperature (SST) and climate oscillations (Beaugrand, 2004; Brander and Mohn, 2004; Clark *et al.*, 2003). However, most studies suggest that other than fisheries, environmental effects would mostly affect the early pelagic stages of cod, which are prone to experience high mortality rates even under favourable conditions (Mcgurk, 1986).

Spawning North Sea cod has consistently been found in specific areas during studies often decades apart (Brander, 1994; Daan, 1978; Harding and Nichols, 1987). The spawning season lasts from January to late April, being progressively later at higher latitudes (Brander, 1994). After an extended period without surveys dedicated to the identification of spawning grounds two surveys in 2004 and 2009, coordinated by the ICES working group PGEGGS (Planning Group on North Sea Cod and Plaice Egg Surveys in the North Sea), were carried out, affording to use recent developments in the field of analysing spatial data to construct statistical models for the egg distribution of cod and three other abundant species of groundfish; haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*) and plaice (*Pleuronectes platessa*).

The decline in recruitment is reflected in the catches of 0-group cod during the IBTS 3rd quarter survey. Settlement, the end of the pelagic stage, may be governed by two main factors. On the one hand it may be the need to consume increasingly larger food items in order to maintain consumption of their preferred relative prey size, which is about 5% of the fish's standard length (Godiksen, 2005; Nielsen and Munk, 1998). Prey in this size fraction may not be present in sufficient numbers and induce the juveniles to include the near-bottom in their search for prey. On the other hand settlement may be induced by a search for territory which offers more protection (Tupper and Boutilier, 1995), as habitats with a more complex relief are beneficial for post-settlement survival (Lough, 2010). Dedicated surveys for research on the early juvenile stage of North Sea cod, like the International 0-group Gadoid Survey (IOGS) from the 1970s and early 1980s, gave a comprehensive overview of the distribution of late pelagic 0-group cod. These were consistently aggregating off the Danish west coast, east of Shetland and east of the Firth of Forth (Holden, 1981). While a later survey series, the 3rd quarter International Bottom Trawl Survey (IBTS),

initiated in 1991, is primarily targeting older stages, juvenile fishes occur in the catch. Hence, the data fed into the DATRAS data base affords to model the potential habitat of newly settled 0-group cod with GAMs. This would allow to identify the characteristics of settling sites and to make an attempt to elucidate whether changes in the distribution of settled juveniles can be explained by changes in the hydrography.

Materials and Methods

Eggs were sampled across the North Sea (Figure 1) by five participating countries during dedicated surveys, or during the annual 1st quarter IBTS. Periods of sampling were from 16th February to 23rd of March 2004, and from 17th January to 6th of March 2009. Juvenile cod was sampled in the 3rd quarter IBTS from 1991 to 2010. While the ichthyoplankton surveys were limited to the North Sea proper, the 3rd quarter survey included the Skagerrak and the Kattegat (Figure 1). Sampling gears were primarily GULF III (Gehringer, 1962; Nellen and Hempel, 1969) and VII (Nash *et al.*, 1998) and BONGO (Posgay and Marak, 1980) for the ichthyoplankton and a GOV-trawl (GOV = Grande Ouverture Verticale), deployed for 10 and 30 minutes double oblique hauls, respectively. To determine cod-like eggs to species level, single eggs were fixed in 96% ethanol or in buffered 0.864% formalin solution and later identified with TaqMan probes (Fox *et al.*, 2008) or cytochrome *b* PCR – RFLP (Lelièvre *et al.*, 2010). Cod-like eggs were then apportioned to the identified species using the derived proportions. Other fish eggs were staged and visually identified to the lowest possible taxonomic level (Ryland *et al.*, 1975; Thompson and Riley, 1981). Finally, the counted numbers were converted to nos. m^{-2} by using filtered volume and sampler depth. Hydrographic data was taken from CTD casts during the ichthyoplankton surveys and augmented with data from the ICES oceanographic data base (ICES 2009). Density as σ_t (kg m^{-3}-1000) was calculated according to UNESCO standards (Millero and Poisson, 1981) and interpolated on a regular 0.25° x 025° grid as were temperature and salinity. The density gradient was calculated in g m^{-3} per nautical mile (NM^{-1}) from the interpolated density.

For 0-group cod the Catch Per Unit Effort (CPUE, nos. h^{-1}) was extracted from DATRAS, together with hydrographic data from the ICES oceanographic data bases (ICES, 2012).

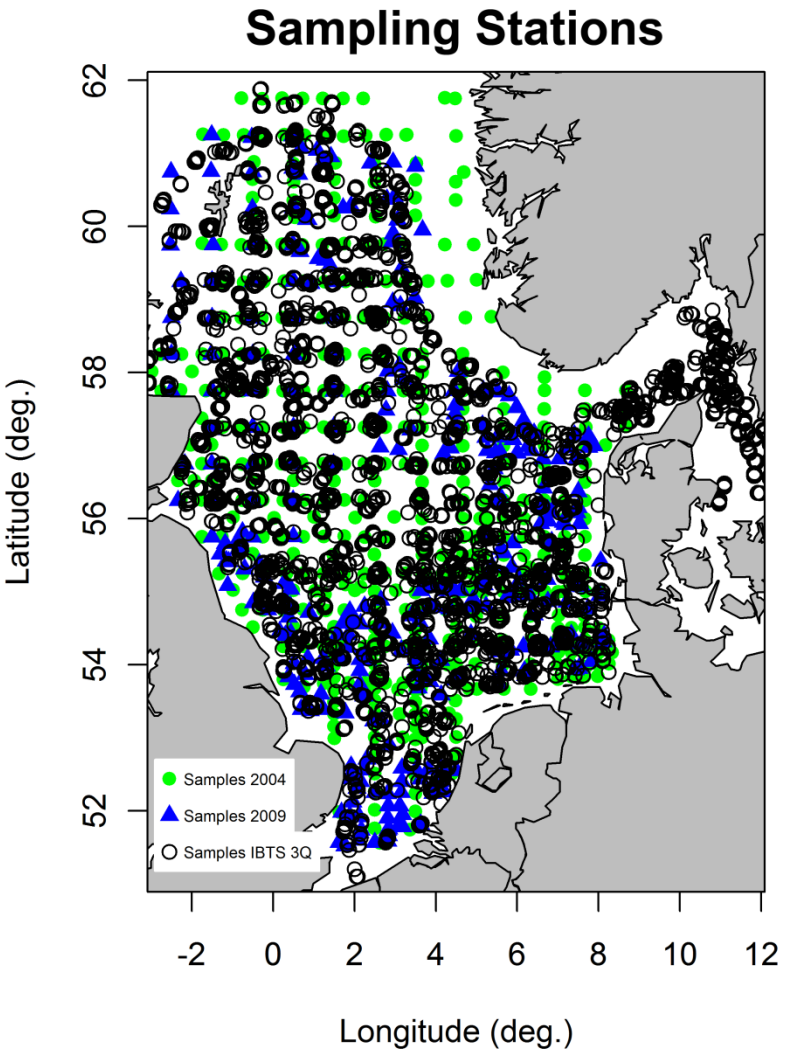

Figure 1: Stations of ichthyoplankton surveys in 2004 (green dots) and 2009 (blue triangles) as well as the stations of the 3rd quarter IBTS surveys for the period of 1991-2010 (open circles). The ichthyoplankton surveys covered only the North Sea proper, while the IBTS surveys also covered the Skagerrak and Kattegat in the East.

For statistical analysis GAM models were constructed in R (R Development Core Team, 2008; Wood, 2001) for presence/absence data, using a binomial model with a logit link and a Gaussian model with an identity link for the log-transformed non-zero abundances, following the general form (after Wood, 2006):

$$g(\mu_i) = \beta_0 + f_1(x_{1i}) + f_2(x_{2i}) + \cdots + f_n(x_{ni}) \quad (1)$$

where g is a known monotonic link function, $\mu i \equiv E(y_i)$ is determined by the explanatory variables x_{1i} to x_{ni}, f_j are smooth functions for these covariates and β_0 is a vector of parameters to be estimated.

For fish eggs, two sets of initial models (Figure 2) for non-zero abundance and presence/absence included spatial dependency, modelled with Principal Coordinates of Neighbour Matrices (PCNM; Blanchet *et al.*, 2008; Borcard and Legendre, 2002), temporal (year, day of the year), bathymetric (bottom depth) and hydrographic variables (temperature, salinity, density gradient). Hydrography was included either for the surface/upper water column or for the bottom, aiming to distinguish the influence of bottom hydrography working through the demersal adults, or of surface hydrography directly influencing the drifting eggs.

As the IBTS survey has some limitations in sampling of juvenile fishes, mainly the large mesh size of the net and limitations in bottom types that can be sampled (Nash, pers. comm.), a statistical model was only constructed for the presence/absence of 0-group cod. Included variables were either temporally stable (location as bivariate term, bottom depth and substrate type) or variable in time (temperature and salinity). The presence/absence of 2-group cod was included as biotic factor, since at this age cod starts to feed on smaller gadoids, while it seasonally still occurs in the same habitat (Riley and Parnell, 1984).

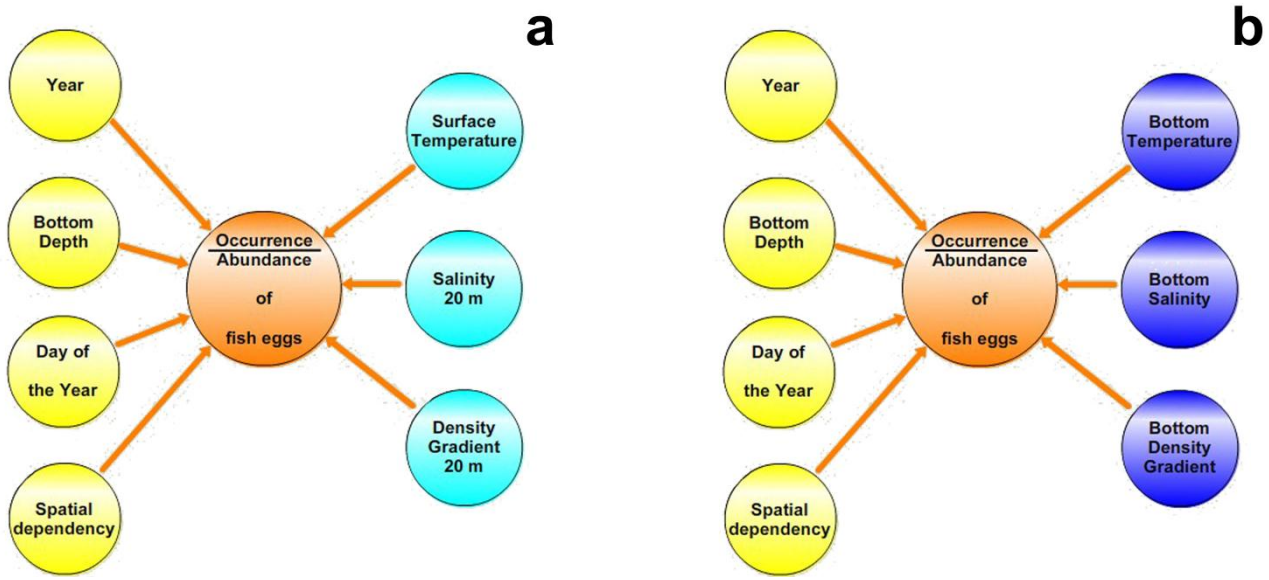

Figure 2: Initial models for the presence/absence and non-zero abundance of fish eggs in the North Sea. Panel **a** depicts the initial model using the hydrographic data for the upper water column, panel **b** depicts the model with the bottom measurements.

The amount of available data limited the validation of the best fitting GAM model for fish eggs to an examination for normality of residuals and patterns therein and in the spread. No such patterns

were found. Post hoc the amount of variation purely explained by each covariate was extracted by variation partitioning with RDA-adjusted R^2 (Peres-Neto *et al.*, 2006).

For 0-group cod it was possible to validate the GAM models by predicting independent data sets. Therefore, GAMs were fitted to the periods 1991-1995, 2001-2005 and 1991-2000 and from these models the presence/absence in the following 5 and 10 years was predicted. These predictions were then evaluated graphically, by interpolation on the same spatial grid as the observations, and statistically with a Taylor diagram.

Results

On a broad scale the winter hydrography in the years 2004 and 2009 was quite similar and also similar to the hydrography presented in earlier studies (Otto and Zimmerman, 1990). Similarly, summer hydrography averaged for four 5-year periods, covering 1991 – 2010, was remarkably stable.

In winter, differences between 2004 and 2009 occurred primarily in the southern North Sea. There, the surface temperature in the German Bight was more than 1°C colder in 2009 and temperatures <5°C extended farther offshore. The influence of freshwater extended farther out to Sea, but density gradients (in g m^{-3} NM^{-1}) were weaker than in 2009.

In summer, the most prominent hydrographic feature was a thermal front, roughly along the 50 m depth contour between the northern tip of Jutland and Flamborough Head, then extending northwards and around the Shetland Isles. Water of temperatures >10°C was south of the front, while cooler water was to the North. Water with salinity >34 entered the North Sea from the North and the South. While the tongue of saline water entering from the English Channel and the 34.5 salinity line were relatively variable, the 35 salinity line never came farther south than about 56°N. Its extension into the Skagerrak however was variable between the periods and appeared to be somewhat reduced in the 2000s. Freshwater influence along the continental coast produced a salinity driven front between coastal waters and the central North Sea.

The broad scale distribution of fish eggs was similar in both years but there were regional variations, mostly occurring in the southern North Sea. The Southern Bight exhibited the highest egg densities (in nos. m^{-2}) in 2009, higher than observed in the rest of the North Sea or in 2004 (Figure 3).

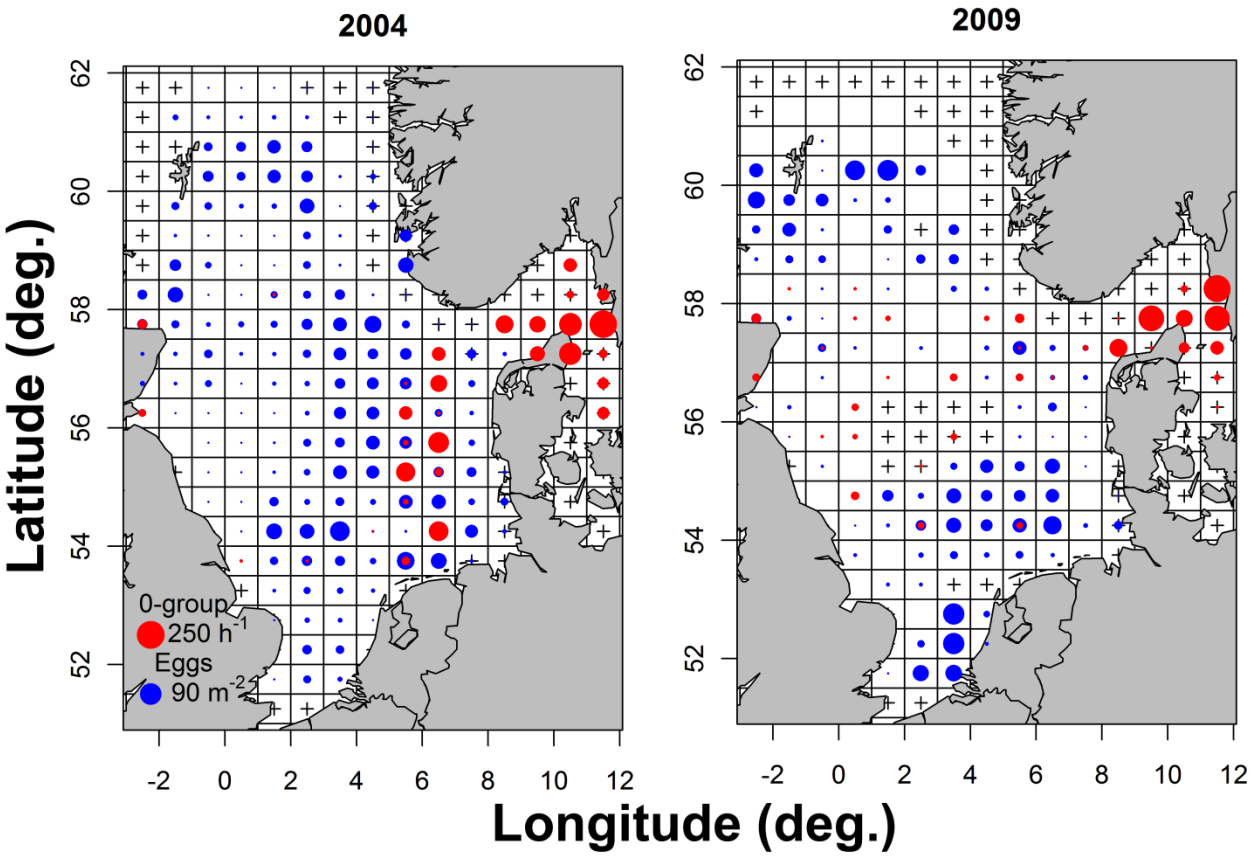

Figure 3: Abundances of cod eggs and 0-group cod in 2004 (left panel) and 2009 (right panel). The reference dots represent the next higher multiple of ten to the maximum abundance. Dots are scaled on a log-scale to make the lowest abundances visible. Crosses indicate ICES squares which were not sampled for either eggs or juveniles in the respective year.

When comparing the statistical models with Akaike's Information Criterion (AIC), abundance models including hydrography for the upper water column were usually superior and explained more of the deviation in the data. The sole exception was haddock, where the model for bottom hydrography fit better. For presence/absence the relationships were more equally distributed with cod and plaice better explained when using bottom hydrography and haddock and whiting having a better fit when using surface hydrography. Variation partitioning showed that combined on all scales spatial dependency explained more of the variation in the abundance data than the environment, while the environment was superior in explaining the variation in presence/absence.

Other than for fish eggs the distribution of 0-group cod changed substantially in the observed period. Catch Per Unit Effort (CPUE) was decreasing, particularly in the offshore areas like the Fisher Banks and East of Shetland. In the German Bight CPUE decreased and the centre of abundance shifted northward along the Jutland coast. In the Skagerrak, a noticeable decrease only occurred in the last period, 2006-2010. The composition of covariates when fitting GAMs to the

presence/absence of 0-group cod was very similar, whether the model was fitted to a 5-year period (1991-1995 and 2001-2005) or to a 10-year period (1991-2000), (Figure 4). In the period 2001-2005 the slope of the bottom was additionally included.

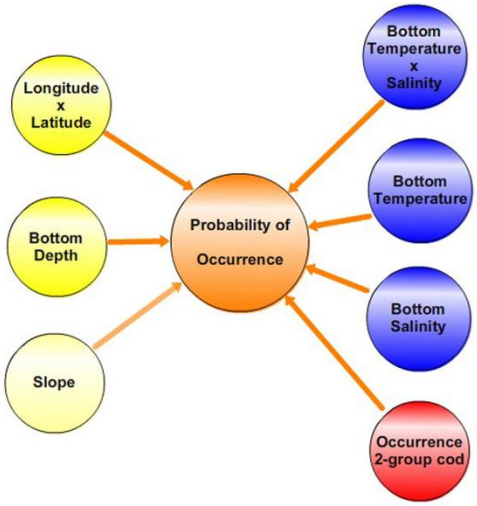

Figure 4: Schematic representation of the best fitting model for the presence/absence of 0-group cod for the periods 1991-1995, 2001-2005 and 1991 – 2000. Slope was only included in the model for the period 2001-2005.

Predicting the next five or ten year period from the fitted GAM, produced fairly good correlation between predictions and observations, although predictions over a shorter time were better (Figure 5), particularly as the prediction for ten years could not fully capture the decline in the probability to find cod in the central and western North Sea during the 2000s.

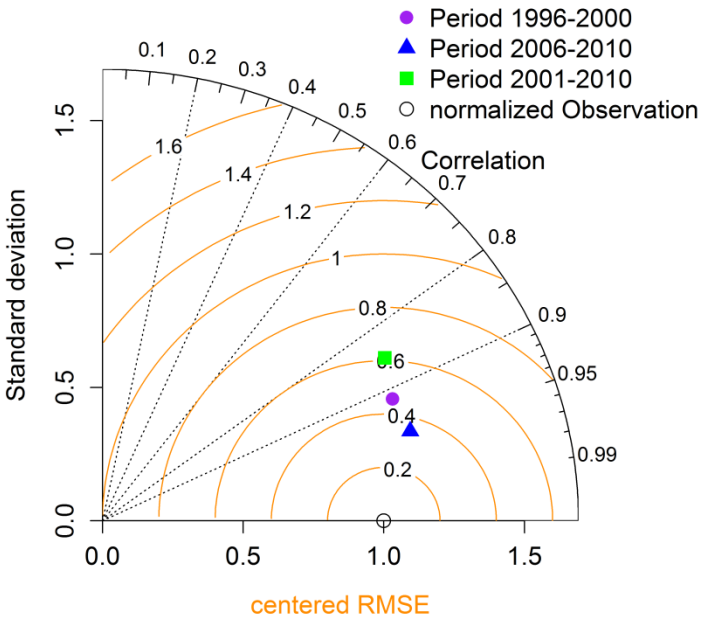

Figure 5: Taylor diagram, comparing the probability of occurrence predicted from the selected GAM models with the observations in 1996-2000, 2006-2010 and 2001-2010. Standard deviation for the observed values was normalized to 1 and the Root Mean Square Error (RMSE) normalized to 0. Standard deviation of the predictions is depicted on the y-axis, while the radii of the circle represent the correlation. The RMSE is plotted on the concentric circles around the normalized standard deviation of the observations. Only the segment of the diagram which depicts the positive correlations is shown.

Discussion and Conclusion

The distribution of spawning grounds in the North Sea, as observed in the course of this study exhibited their persistency over time, as it was similar to earlier studies (Brander, 1994; Daan, 1978; Saville, 1959). Considering that genetically distinct sub-populations were recently identified (Hutchinson *et al.*, 2001), it appears that on the broad scale cod are bound to return to a specific spawning ground. Locally, within spawning grounds, there is some adjustment to prevailing hydrographic conditions, as was apparent in the southern North Sea in relation to the front between freshwater influenced water along the continental coast and the oceanic water farther out to sea. Controls on presence/absence were primarily environmental, while the abundance relied more on spatial dependency. However exceptions from this rule are possible. Haddock, which, when adult, is limited by its environmental preferences to the northern North Sea (Hedger *et al.*, 2004), exhibited a particularly high explanatory power of the environment for the abundance. This might be due to the limitation by the environment, as the opposite case (large influence of spatial dependency in comparison to environment) has been shown for plaice (Loots *et al.*, 2010), which is well within its environmental range in the North Sea. The apparently higher influence of surface hydrography on abundance indicates that the eggs are primarily transported in the upper water column.

The stable hydrography over most of the North Sea in the study period indicates that the observed changes in CPUE and distribution of 0-group cod can only be partially explained by the hydrographic conditions, or alternatively by changes in hydrography that have occurred before the study period (c.f. Beaugrand, 2004) which influenced the distributional patterns of 0-group cod during the following years. That CPUE in the Skagerrak was stable over a longer period may be due to inflow of 0-group cod from the North Sea, as was suggested in previous studies (Stenseth *et al.*, 2006; Svedäng and Svenson, 2006). Including only external covariates into a model of the juveniles' habitat appeared useful, as it provided good prediction on sub-decadal time scales. Hydrographic variables (temperature, salinity) apparently served as modifiers for the influence of time invariable covariates, i.e. geographic positions and bottom depth.

In comparison, the statistical models for fish eggs emphasized that the influence of changes in temperature would likely be larger than that of salinity. An increase in temperature may accelerate egg development (Thompson and Riley, 1981), influencing the location upon hatching and thus may not guarantee that the larvae hatch into favourable conditions. For the juveniles, salinity appears somewhat more important than temperature. Typical settling areas, were relatively shallow, warm and low in salinity, conditions which promote spatial separation from older, cannibalistic,

conspecifics (Riley and Parnell, 1984). Hence, conditions which may cause increased mortality of cod eggs and later on larvae may have benefits for juvenile cod.

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